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THE PTYCHOCYST, A MAJOR NEW CATEGORY OF CNIDA USED IN TUBE CONSTRUCTION BY A CERIANTHID ANEMONE

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The cerianthid anemones characteristically are burrowing forms, living in a tube of their own construction. It has been known for many years now that the tube of cerianthids is at least partially composed of discharged nematocysts along with various "foreign objects" including substrate material from the vicinity of the tube (*e.g.*, McMurrich, 1890; Hyman, 1940; Frey, 1970). However, no one to date appears to have examined critically the mechanism of tube formation in cerianthid cnidarians, nor the type(s) of nematocysts and the extent to which they might be involved. The general sentiment regarding this problem was probably best summarized by Torrey and Kleeberger (1909, p. 117) who stated, "There is little to be said of the sheath with which the animal readily surrounds itself. It serves as a lining for the burrow, is composed of a feltwork of nematocysts and is easily torn."

Carlgren (1912, p. 28) mentioned the extremely large nematocysts (up to 103 μm capsule length) with the "coiled spiral thread" which were extremely common in the column ectoderm of various cerianthids. Carlgren (1940, p. 15) later identifies these as "atrichs" and indicates they are the most numerous cnidae present on the column of cerianthids and that both holotrichs and spirocysts are rare in the same region. More recently, Schmidt (1972, 1974) has identified the nematocysts in the tubes of cerianthids as "atrichs."

In the present study, the so-called atrichous isorhiza (*i.e.*, atrich) involved in tube formation by a cerianthid anemone has been examined using a variety of microscopical methods. Rather than being an atrich, this cnida represents an entirely new, major category of coelenterate organelle which has heretofore been undescribed. Contrary to all nematocysts and spirocysts studied to date, this new cnida is not helically folded within the capsule prior to discharge. Instead, it exhibits an entirely new method of folding of the undischarged thread resulting in a variable number of pleats in circumference, but entirely lacking pleats in length.

Materials and Methods

The species examined in the present study was *Ceriantheopsis americanus* Verrill, 1864) collected from the Alligator Point area of the north Florida Gulf Coast. For scanning electron microscopy (SEM), an entire *Ceriantheopsis* with a freshly formed tube was fixed in Parducz's (1967) fixative for one hour. Following fixation, a portion of the column containing the newly formed tube was excised and transferred to a 16% glycerol solution for 24 hours and then prepared for Freon critical point drying following the procedures given in Mariscal (1974a, b). The prepared tissues were then mounted, coated with gold-palladium in a Denton vacuum evaporator and examined in a Cambridge S4-10 scanning electron microscope.

For transmission electron microscopy (TEM), small portions of the mid-column epidermis in the region of tube formation were dissected out and this plus freshly secreted tube material were fixed in cold 2% glutaraldehyde in sea water for one hour, post-fixed in 2% OsO_4 in sea water for 30 minutes and stained in 2% uranyl acetate for 5 minutes. Following dehydration in a graded acetone series, the material was embedded in Epon, thin sectioned and examined in a Phillips 200 transmission electron microscope.

Light microscopy was done on a Reichert Zetopan phase contrast microscope with a Nikon AFM photomicrographic attachment.

Results

Tube construction

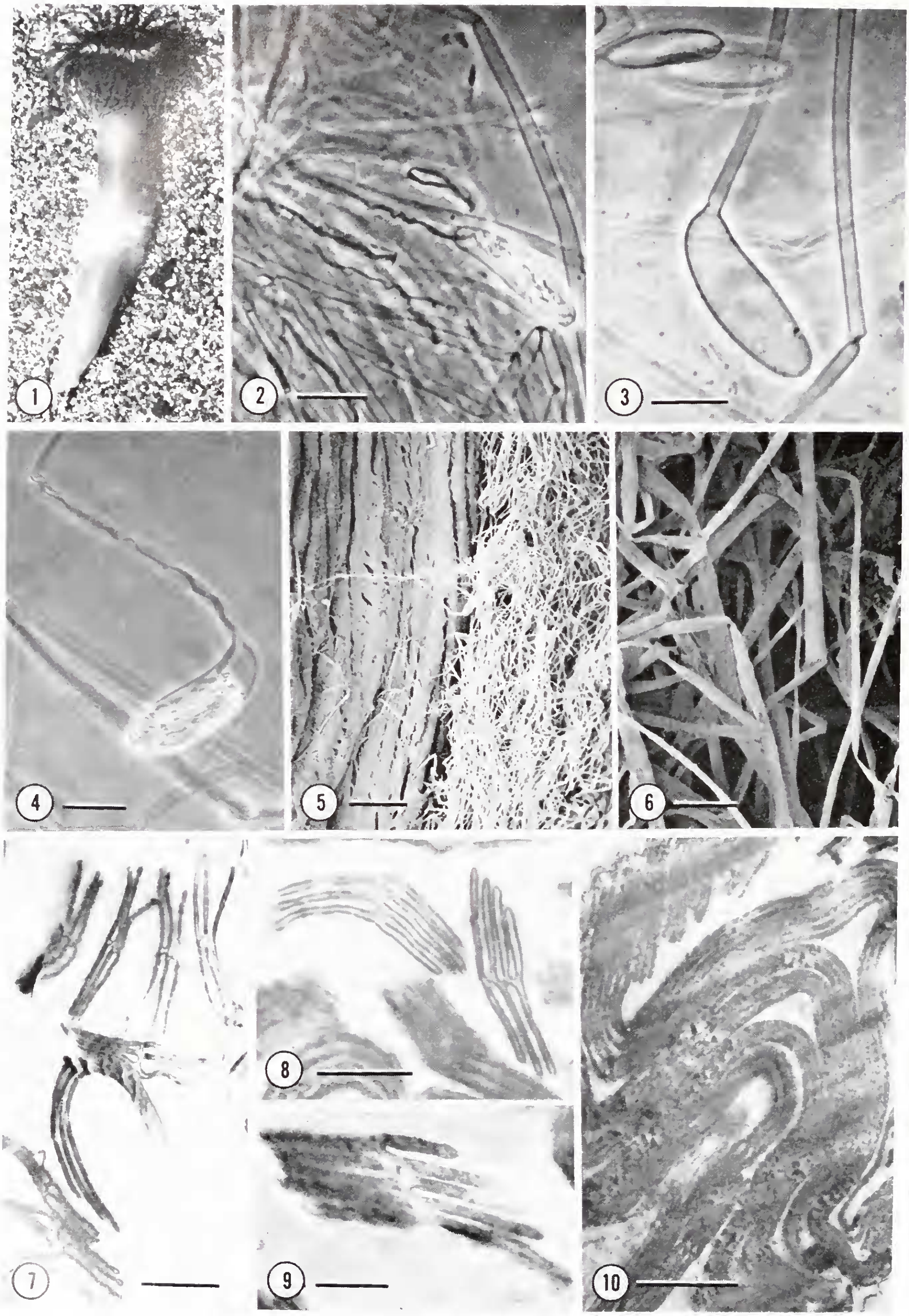
Within minutes of removing *C. americanus* from its tube, one can notice the formation of a fine, white sheath, representing the incipient new tube, enveloping the exposed column ectoderm (Fig. 1). About five minutes after tube removal, it is possible to see long, white filaments radiating out from the column ectoderm (Fig. 1). Examination of these filaments as well as the newly formed tube material under the light microscope showed a dense mat of the intertwined threads and capsules of thousands of discharged cnidae (Figs. 2, 3). Although several types of typical nematocysts (including holotrichous isorhizas and microbasic b-mastigophores) and spirocysts were present in the tube material, by far the vast majority of the cnidae present belonged to a new, undescribed category to which has been given the name of "ptychocyst."

Ptychocyst diagnosis

Undischarged thread not helically folded, with a variable number of pleats in circumference but no pleats in length; discharged thread long, non-isodiametric and with a variable number of fine ridges running along its length representing the folds by which it is compressed in diameter prior to discharge; thread tip closed and entire thread lacking in spines or hollow tubules; undischarged and partially discharged threads both basophilic and acidophilic. Name derived from Greek *ptychos* meaning fold.

Dimensions of capsule and thread

The ptychocysts are extremely variable in size, but are much larger than the spirocysts or mastigophores present. Carlgren (1912) mentions that the capsule of this cnida reaches a length of 70 μm and later (1940) gives the size range for apparently the same cnida (which he calls an "atrich") as being 36–82 μm in length and 12–25 μm in width. Measurements of ptychocysts in the present study revealed a range of 29–75 μm in length and 8–36 μm in width. However, there appeared to be two distinct size classes with the largest yielding measurements of 59–75 $\mu m \times$ 19–36 μm and the smallest being 29–36 $\mu m \times$ 8–12 μm in size.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Measurements of 20 cnidae in each size class gave mean values of 65 μm in length $\times$ 27 μm in width for the largest examples and 32 μm $\times$ 10 μm for the smallest ones. In other cerianthids, what appears to be this same cnida may be even larger since Carlgren (1940) mentions that the "atrichs" on the column of *Pachycerianthus multiplicatus* had a size of 113 $\times$ 43 μm, making them among the largest cnidae known.

The capsules of ptychocysts, with widths varying from 25% to 55% of the capsule length, tend to be broader than those of many anthozoan cnidae. However, the capsules appear to be bilaterally compressed, at least in the larger cnidae, and thus the above range of measurements probably reflects the orientation of the capsule under the microscope at the time of measurement.

The threads of ptychocysts are non-isodiametric and in large examples taper from about 5 μm near the capsule to about 2 μm at the closed tip for a total reduction in diameter of some 2.5 times. The discharged threads may be extremely long (over 2 mm in length) and with the naked eye can be seen projecting outwards from the column ectoderm during new tube formation (Fig. 1).

Mechanism of discharge and general characteristics of the thread

Like all nematocysts and spirocysts examined to date (*e.g.*, see Mariscal, 1974c and Mariscal and McLean, 1976), ptychocysts evert during discharge (Fig. 4). Although some threads appear to emerge more or less in line with the capsule, many others evert at an angle of about 60 to 90 degrees with the plane of the capsule (*e.g.*, Figs. 3, 4). If the capsules are oriented perpendicular to the column surface (as they appear to be), this is perhaps an adpatation to facilitate the intertwining of the discharging threads at various levels above the column surface in order to form a stronger, more tightly interwoven tube. The newly everted threads are apparently sticky since sand and other sedimentary material in the vicinity adheres to the discharged threads, thus becoming incorporated in the outer matrix of the new tube. Their adhesive properties probably tend to bond

FIGURE 1 Photograph of *Ceriantheopsis americanus* in process of secreting new tube. Animal is about 15 cm long.

FIGURE 2. Photomicrograph of newly formed tube material removed from the column of *C. americanus*. Note everting ptychocyst among the capsules and threads of previously fired ptychocysts. Scale bar is 20 μm.

FIGURE 3. Photomicrograph of discharged ptychocyst capsule and thread. Scale bar is 20 μm.

FIGURE 4. Photomicrograph of everting ptychocyst. Note the arrangement of the uneverted thread within the capsule. Scale bar is 20 μm.

FIGURE 5. SEM of interface between column (left) and region of new tube formation (right). Scale bar is 200 μm.

FIGURE 6. SEM of newly everted ptychocyst threads forming felted meshwork of new tube. Note longitudinal ridges on the threads. Scale bar is 20 μm.

FIGURE 7. TEM, primarily of cross-sections of undischarged ptychocyst threads with 6 pleats. The strongly curved thread is a partial longitudinal section. Scale bar is 1 μm.

FIGURE 8. TEM cross-section of undischarged ptychocyst threads with 7 pleats. Scale bar is 0.5 μm.

FIGURE 9. TEM cross-section of undischarged ptychocyst thread with 10 pleats. Scale bar is 0.5 μm.

FIGURE 10. TEM longitudinal section of undischarged ptychocyst threads, probably with 6 pleats. Scale bar is 1 μm.

the everted threads to each other as well, again aiding in strengthening the tube as it forms.

The undischarged and partially discharged threads of ptychocysts stain with both basic (methylene blue, toluidine blue)and acid dyes (acid fuchsin). Since nematocysts have been classically considered to be basophilic in nature and spirocysts acidophilic (Hyman, 1940), the fact that ptychocysts are both basophilic and acidophilic may suggest some chemical differences between them and the other cnidae described to date. However, the nonspecificity of such stains in the case of many coelenterate cnidae indicates that more critical tests need to be made before much can be said concerning possible chemical differences.

Examination with SEM of the column surface of *C. americanus* in the region of new tube formation clearly shows the mass of newly fired ptychocyst threads forming the tube (Fig. 5). An enlarged view of these threads reveals that they lack any form of spination or tubules and instead have longitudinal ridges or striations running along their length, a feature previously unknown for coelenterate cnidae (Fig. 6). These ridges, representing the folds by which the thread is compressed in diameter prior to discharge, can also be seen with the phase contrast microscope, but have been heretofore undescribed.

Ultrastructure of the undischarged thread

TEM examination of the threads of undischarged ptychocysts revealed that they have a previously undescribed method of folding. All undischarged nematocyst and spirocyst threads examined to date with TEM are helically folded with multiple pleats in length, but only three in circumference. The undischarged ptychocyst thread, on the other hand, is folded accordion-like in circumference into a series of stacked pleats of varying number (Figs. 7, 8, 9). Following the terminology of Skaer and Picken (1965), the term "fold" is used to refer to the region where the surface of the thread is in fact folded, while "pleat" refers to the two thickness of the thread brought together by folding.

Due to the great variability in folding, the various types of ptychocyst threads have been categorized based on the number of pleats they contain. In the case of undischarged threads which are all infolded towards a common medial axis, the number of pleats occurring along both sides of this axis must be counted. Figure 7, for example, shows cross-sections of a symmetrically folded thread which has formed 6 pleats. Figure 8 shows an asymmetrically folded thread forming a total of 7 pleats, and Figure 9 shows a symmetrically folded thread with 10 pleats.

Another unique feature of the undischarged ptychocysts thread relates to its lack of pleating in length (Fig. 10). The threads of all spirocysts and nematocysts examined with TEM are complexly pleated, accordion-like, in length. When these cnidae discharge, the pleats become smoothed out allowing a significant increase in length of the everted thread to form a hollow cylinder (Skaer and Picken, 1965; Mariscal, 1974c). The ptychocyst thread, however, is not pleated in length and thus the length of the undischarged thread within the capsule should equal that of the fully everted thread, although it has not been possible to measure this accurately (Fig. 10).

This lack of pleating in length of the undischarged thread suggests that the ptychocyst thread may be arranged within the capsule differently than are spirocysts and nematocysts and preliminary observations suggest this to be the case. The undischarged threads of spirocysts and many nematocysts are spirally coiled around the circumference of the capsule and surrounding the central shaft region, when present. The thread of the ptychocyst, on the other hand, is arranged in the longitudinal plane of the capsule in a manner very reminiscent of the way a fire hose or ship's line is laid down to permit easy running without entanglement (Figs. 2, 4).

Ultrastructure of the capsule tip

Neither an operculum nor apical flaps is present on the capsule tip, at least in the form that these structures have been previously described for hydrozoan and anthozoan nematocysts, respectively (Fig. 11). Instead, the apical tip of the capsule appears to be folded together and sealed along several suture planes, perhaps three, although the number remains to be determined accurately. Figure 11 shows two of the triangular apical folds and one of the ruptured suture planes between them.

Ultrastructure of the discharged thread

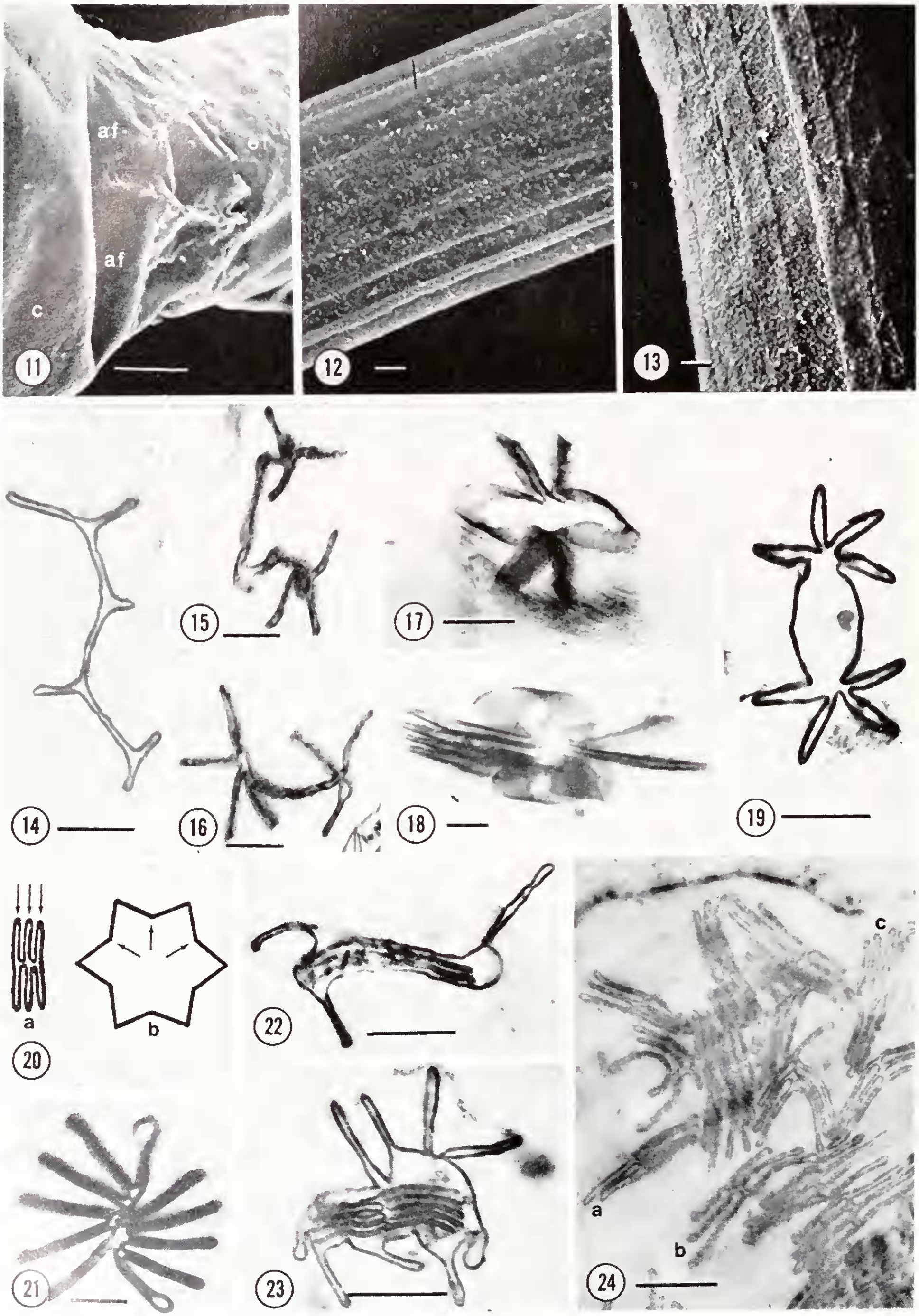
SEM of the discharged ptychocyst thread clearly shows the remarkable longitudinal ridges along which the thread is folded and compressed in diameter prior to discharge (Figs. 6, 12–13). The relief of these ridges permits the reconstruction of the method of thread folding prior to discharge, as well as allowing a tentative count of the number of pleats present (Fig. 13).

TEM of newly formed tube material provided numerous cross-sections of ptychocyst threads. Nearly all of the sectioned threads were collapsed to some degree so that the lumen was often indistinct (Figs. 14–18). In some cases, one portion of the thread would be partially inflated and another portion collapsed (Figs. 17, 18). Many of the threads had a small star or double star configuration, either collapsed (Figs. 15, 16) or partially expanded (Fig. 19).

Construction of paper models of ptychocyst threads allowed a comparison of the different patterns of pleating before, during and after discharge. Figure 20 diagrammatically shows a thread with 6 pleats both before and after discharge. Although the tip of a pleat on an uneverted thread represents a fold between the base of two pleats on the discharged thread (arrows), the same number of pleats occurred in both the undischarged and discharged state and were of equal width at any particular point on the thread (Fig. 20).

One of the most perplexing initial findings of the present study concerned the great variability in pleating in circumference of the thread, both undischarged and discharged. All undischarged nematocyst and spirocyst threads examined to date have been helically folded in essentially similar fashion and contain only three major pleats in circumference. However, from 5 to a maximum of 11 pleats (Fig. 21) have been identified in the material examined in the present study, and it is predicted that a greater range in pleating in circumference will be found for this cnida, perhaps 3 or 4 to 12.

Our preliminary measurements from a variety of preparations suggests that the widths of individual pleats may be relatively consistent. In the case of two



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different threads, each containing 11 pleats, it was found that the width of the everted pleats in a SEM preparation (Fig. 12) was the same as that observed in a TEM preparation (Fig. 21). In both, the mean width of a single pleat was about 0.85 μm, this being nearly identical to the mean width of pleats from all preparations measured in the present study.

Cross-sections through everting threads were especially useful in such measurements and for comparative purposes. For example, Figure 22 shows a cross-section through an everting thread containing 5 pleats, while Figure 23 shows an everting thread with 9 pleats. Note in Figure 23 that there are clearly 9 pleats on both the uneverted and everted sections at that particular point along the thread's length.

Although it was first assumed that the number of pleats would at least be consistent within a single capsule, TEM sections have revealed that a variable number of pleats can occur on a single thread. For example, Figure 24 shows an undischarged thread with 5, 6, and 7 pleats.

The consistent width of each pleat and the variable number occurring on a single thread has suggested how a nonhelically folded thread can taper in the same fashion as a helically pleated thread. If in fact the pleat width is relatively constant regardless of the number of pleats present, then a simple reduction in the number of pleats from the base of the thread to its tip could account for the

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FIGURE 11. SEM of opercular region of discharged ptychocyst capsule (c) showing apical folds (af) and ruptured suture plane between them through which the everting thread (et) passes. Scale bar is 1 μm.

FIGURE 12. SEM of everted ptychocyst thread, probably with 11 pleats, showing the pronounced longitudinal ridges by which the thread is folded in diameter prior to discharge. The fine granules may represent adhesive material. Scale bar is 1 μm.

FIGURE 13. SEM of surface of everted ptychocyst thread, probably with 8 pleats, showing relief and folding pattern of pleats. Scale bar is 1 μm.

FIGURE 14. TEM cross-section of collapsed, everted ptychocyst thread, probably with 7 pleats. Scale bar is 1 μm.

FIGURE 15. TEM cross-section of collapsed, everted ptychocyst thread with 10 pleats. Scale bar is 1 μm.

FIGURE 16. TEM cross-section of collapsed, everted ptychocyst thread, probably with 9 pleats. Scale bar is 1 μm.

FIGURE 17. TEM cross-section of everted, partially collapsed ptychocyst thread with 6 pleats. Scale bar is 1 μm.

FIGURE 18. TEM cross-section of everted, partially collapsed ptychocyst thread, probably with 8 pleats. Scale bar is 1 μm.

FIGURE 19. TEM cross-section of everted, partially expanded ptychocyst thread with 10 pleats. Scale bar is 1 μm.

FIGURE 20. Diagram illustrating eversion of ptychocyst thread: (a) cross-section of undischarged ptychocyst thread with 6 pleats; (b) cross-section of expanded ptychocyst thread with 6 pleats following eversion. The arrows point to the same folds, both before and after discharge.

FIGURE 21. TEM cross-section of everted, collapsed ptychocyst thread with 11 pleats. Scale bar is 0.5 μm.

FIGURE 22. TEM cross-section of ptychocyst thread, probably with 5 pleats, in the process of everting. Scale bar is 1 μm.

FIGURE 23. TEM cross-section of ptychocyst thread with 9 pleats in the process of everting. Note the same number of pleats on both the uneverted and everted portions of the same thread. Scale bar is 1 μm.

FIGURE 24. TEM of cross-sections of ptychocyst threads with variable number of pleats within the same capsule: (a) thread with what appears to be 5 pleats; (b) thread with 6 pleats; and (c) thread with 7 pleats. Scale bar is 0.5 μm.

observed tapering of the thread. Thus, in the case of the largest ptychocysts observed (about 75 μm capsule length in the present study), perhaps a full range of pleating occurs, whereas in the smaller ptychocysts perhaps a reduced range of pleating will be found. However, more extensive measurements will be necessary in order to verify this.

The ptychocyst thread is totally devoid of spines and, as such may represent one of the few cases of a truly atrichous cnida (Figs. 12, 13). Although no regular pattern of anything which could be interpreted as spination is present, light microscopy and SEM of everted ptychocyst threads often show a variety of fine granular material adhering to the thread surface. Since the everted threads are very sticky, it is possible that these granules represent the adhesive material (Figs. 12, 13), although at present the possibility cannot be ruled out that the granules are artifactual in nature.

The general features of the ptychocyst capsule and thread and mechanism of discharge are summarized in Figure 25.

It should be mentioned here that although the ptychocyst possesses a unique method of folding, the spirocysts and nematocysts (including holotrichs and microbasic mastigophores) also present on the column of *C. americanus* had the typical tripartite, helical folding of the thread in circumference and the characteristic accordion-like pleating of the thread in length similar to the cnidae from other species of anthozoans.

Discussion

Although it has been known for many years that ceriantbids incorporated discharged cnidae into the construction of the tubes which surround them, the identification and relative importance of these cnidae has remained unclear. It has been determined in the present study that the cnida involved in tube construction by *Ceriantheopsis americanus* represents a major new category, the ptychocyst, and that it is primarily, if not entirely, responsible for the strength and formation of the tube. The "stickiness" and interweaving capability of the long ptychocyst thread forms a tube of extreme toughness and resiliency, as well as allowing for the incorporation of sand and other sedimentary material into the outer matrix of the tube. The layered construction of the *C. americanus* tube suggests that ptychocysts are periodically added to the inside of the tube during the life of the animal. Exactly how the tube can increase in diameter to accommodate the growth of the animal remains unclear.

Some workers have indicated that spirocysts contributed to tube construction in cerianthids (*e.g.*, Robson, 1973). The present study found that spirocysts are indeed present in the newly secreted tube material of *C. americanus* but are rare compared to the tremendous numbers of ptychocysts present. Similarly, both large holotrichous isorhizas and smaller microbasic mastigophores are present in the newly secreted tube, but light and electron microscopy reveals that these nematocysts, like the spirocysts, are relatively rare. It is therefore concluded that the role of these cnidae in tube formation is negligible compared to that of the ptychocyst, at least in the case of *C. americanus*.

Aside from their function in cerianthid tube construction, the ptychocysts are completely different from all other nematocysts and spirocysts described in regard

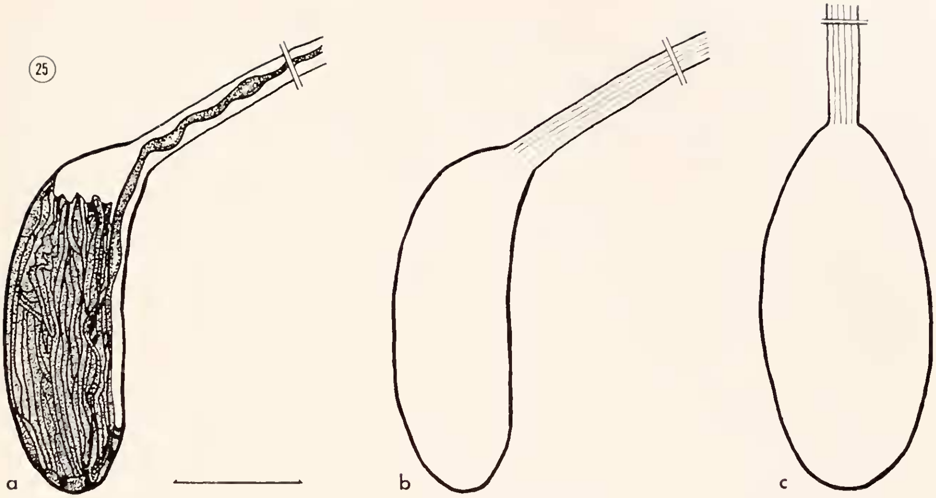

FIGURE 25. Diagram illustrating general characteristics of the ptychocyst capsule and thread: (a) side view of ptychocyst in the process of everting during discharge (note method of unfolding of everting thread); (b) side view of fully discharged ptychocyst showing longitudinal ridges on the thread representing the folds by which the thread is compressed in diameter prior to discharge; (c) frontal view of approximately the same size ptychocyst capsule as shown in (b). Scale bar is 22 μm.

to the method of folding of the thread, both before and after discharge. All spirocysts and nematocysts examined to date with the electron microscope possess a helical, tripartite pleating of the undischarged thread in circumference and an accordion-like pleating of the thread in length (*e.g.*, Mariscal, 1974c; Mariscal, Bigger and McLean, 1976; Mariscal and McLean, 1976). The ptychocyst thread, on the other hand, is not helically folded and is therefore not compressed and pleated at all in length. This points out several important differences in the functional significance and evolution of coelenterate cnidae.

In the case of a helically pleated thread, there is a significant reduction in the length and diameter of the undischarged thread which allows for it to be packed into a relatively small capsule. Helical folding thus allows for the expansion in three dimensions of an everting spirocyst or nematocyst thread, as well as imparting a rotary motion to it, somewhat analogous to the motion imparted to a bullet by the rifling of a gun barrel (Skaer and Picken, 1965).

On the other hand, nonhelical folding, characteristic of the ptychocyst, allows for an expansion of the thread in only two dimensions since there is no pleating in length. Thus the discharge of a ptychocyst thread involves a flattened belt of material (the uneverted thread) passing up through a hollow tube. By the very nature of its folding, one would not expect a strong rotary or boring motion to be imparted to the ptychocyst thread during discharge. However, the thread does appear to twist during eversion and there may be a slight rotary component associated with ptychocyst discharge as well.

With regard to classification of ptychocysts within the classical framework of coelenterate cnidae, many more questions than answers have been raised by the present study. According to the most widely used classification scheme, that of Weill (1929, 1930, 1934) as modified by Werner (1965) and Mariscal (1971, 1974c), there are two major categories of coelenterate cnidae: nematocysts and spirocysts. Based on differences in their chemical properties and structure, recent workers have generally agreed with Weill's separation of spirocysts from nematocysts proper (*e.g.*, Westfall, 1965; Schmidt, 1969, 1974; Mariscal, 1974c; Mariscal and McLean, 1976). In spite of their well known differences, however, both spirocyst and nematocyst threads have identical methods of folding and pleating within the capsule in the undischarged state. If, as is generally acknowledged, spirocysts and nematocysts are distinct enough to be placed in separate, major categories, then it seems clear that the ptychocyst represents a third major category of coelenterate cnidae in both Weill's (1934) and Schmidt's (1974) classification schemes.

Several other possibilities concerning the classification of the ptychocyst have also been considered in the present study. For example, based on light microscopical observations, the ptychocyst thread tip appears to be closed, suggesting possible affinities with nematocysts belonging to the Astomocnidae. However, the ultrastructure and method of folding of the undischarged thread has not been examined in detail in astomocnid nematocysts. Only one astomocnid nematocyst, the desmoneme, has been examined to date with TEM (Chapman and Tilney, 1959) and SEM (Mills and Mariscal, unpublished). It appears from these studies that the method of folding of desmonemes is not the same as for ptychocysts. Furthermore, all astomocnid nematocysts have been described to date only from hydrozoans. The fact that the ptychocyst occurs only in anthozoans (so far as is known) might be further evidence suggesting caution in placing the ptychocyst in the Astomocnidae until more is known about the ultrastructure of this group of nematocysts.

Another possibility is that the ptychocyst is a kind of atrichous isorhiza based on the complete absence of spination on the thread. This cnida has in fact been called an atrich by Schmidt (1972, 1974) and Carlgren (1940). Atrichs, however, have been classically considered to belong to the Stomocnidae which have threads open at the tip. The observation that the ptychocyst thread is closed at the tip would argue against ptychocysts being considered as a new type of atrich. In addition, all atrichs examined to date with the electron microscope have been found to possess spines along the length of the thread, and thus are actually holotrichous (Westfall, 1965; Schmidt, 1969, 1974; Bigger, 1976). It is therefore questionable if a truly atrichous stomocnid nematocyst exists. If in fact all previously described atrichous isorhizas are holotrichous, then the ultrastructure and method of folding of holotrichous isorhizas might profitably be examined and compared with that of ptychocysts.

Fortunately there have been several detailed examinations by TEM of the ultrastructure of the undischarged holotrich thread and it is clear that it is helically folded and pleated (Skaer and Picken, 1965; Mariscal, 1974c and unpublished). Although relatively rare, holotrichs also occur on the column of *C. americanus*, and they too are helically folded (Mariscal and Bigger, unpublished). Therefore, there seems to be no close affinities between the structure of ptychocysts and that of atrichous isorhizas or holotrichous isorhizas as classically described.

Studies are currently underway concerning the nature of the possible sensory structures associated with ptychocysts. Preliminary examination of the column of *C. americanus* with both TEM and SEM suggests that a single cilium surrounded by a circlet of shorter stereocilia is closely associated with the tip of undischarged ptychocysts. Multiciliated cells appear to surround the ptychocyte although their relationship to the ptychocyte and the discharge process, if any, is not yet clear.

To summarize the systematic status of the ptychocyst in relation to both nematocysts and spirocysts, the following revision in the classification of coelenterate cnidae by Mariscal (1974c) is proposed.

I. HELICOPTYCHONEMES—undischarged thread helically folded to form multiple pleats in length and three pleats in circumference
  A. Nematocysts—thread spined or unspined but without hollow tubules
    1. Astomocnidae—thread closed at the tip
    2. Stomocnidae—thread open at the tip
  B. Spirocysts—thread lacking spines but with hollow tubules
II. HETEROPTYCHONEMES—undischarged thread not helically folded, with a variable number of pleats in circumference but none in length
  A. Ptychocysts—thread lacking both spines and hollow tubules but with longitudinal ridges along its length

Although the ptychocyst is the first major new category of coelenterate cnida to be discovered since the spirocyst was recognized and named by Bedot in 1890, it is entirely possible that additional major new categories of cnidae remain to be recognized, perhaps among the Astomocnidae. Therefore, the above proposed revision in the classification of coelenterate cnidae has been set up to allow for the addition of new categories or sub-categories as they might be discovered. It is predicted that the threads of all toxin delivering nematocysts, presently belonging to the Stomocnidae, will turn out to be helically folded and pleated, but that some re-classification of the Astomocnidae may be necessary once these latter cnidae are examined in detail with the electron microscope.

The completely unexpected and unusual method of folding and pleating of the ptychocyst thread emphasizes the need for further study of the structure, function, mechanism of discharge, toxicology and biochemistry of the unique intracellular organelles of coelenterates which are probably among the most complex known in the animal kingdom.

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Summary

Light, transmission electron and scanning electron microscopy of a ceranthid anemone reveal that the protective tube with which the animal surrounds itself

is composed almost entirely of discharged, interwoven cnidae of a heretofore undescribed type.

As opposed to the threads of all nematocysts and spirocysts described to date, the thread of the new cnida, to which has been given the name of ptychocyst, is not helically folded, forming a variable number of pleats in circumference (from 5 to 11 observed in the present study), and no pleats in length. The discharged threads are quite long (over 2 mm in some) and are non-isodiametric, tapering from a diameter of about 5 μm at the base to about 2 μm at the tip for an overall reduction in diameter of 2.5 times.

The everted thread has a number of fine ridges running along its length which can be seen using phase contrast microscopy and which represent the folds by which the thread is compressed in diameter. The thread tip is closed and the entire thread is unarmed, lacking both spines and hollow tubules. The undischarged and partially discharged threads are both basophilic and acidophilic. The capsules are bilaterally compressed and are often large (up to 75 μm long and 36 μm wide) with perhaps two distinct size classes.

The completely unique method of thread folding indicates that ptychocysts are significantly different from either nematocysts or spirocysts, both of which have helically folded and pleated threads. Ptychocysts have therefore been included in the classification of coelenterate cnidae as a third major category, equal in rank to both nematocysts and spirocysts.

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